

Prediction of Breeding Values for Tenderness of Market Animals from Measurements on Bulls¹

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ABSTRACT: Data were tenderness measures on steaks from 237 bulls (Group II) slaughtered after producing freezable semen and on 1,431 related steers and heifers (market animals, Group I) from Angus, Hereford, Pinzgauer, Brahman, and Sahiwal crosses from the Germ Plasm Evaluation project at the U.S. Meat Animal Research Center. Tenderness was assessed through Warner-Bratzler Shear Force (SF), taste panel tenderness (TPT), marbling score (MS), and myofibrillar fragmentation index (MFI). For all traits, as fraction *Bos indicus* inheritance increased, implied tenderness decreased. Heritability estimates were generally not significantly different from zero. Genetic correlations generally indicated favorable associations among the traits. The range in predicted

breeding values of bulls for market animal tenderness was small and from $-.34$ to $.32$ kg for market animal shear force. Because of low estimates of heritability for SF or TPT, results from this experiment indicate that selection based on tenderness of steaks sampled from intact or late castrate males slaughtered following collection of freezable quality semen would not be very effective in improving average tenderness of steaks from steers or heifer progeny. If a mean of heritability estimates reported in the literature of $.27$ for shear value was assumed for market steer and heifer progeny instead of $.02$ as found in the present study, then selection based on estimates of shear force in young bulls would be relatively more effective in improving shear force of market progeny.

Key Words: Carcass Quality, Meat Quality, Crossbreeding, Selection

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Introduction

Bos indicus cattle and *Bos indicus* \times *Bos taurus* crosses often are more productive than British and continental breeds in tropical and semitropical climates, because of heat tolerance and disease and parasite resistance (Turner, 1980). Although *Bos indicus* breeds may improve efficiency and components of lifetime production when crossed with *Bos taurus* cattle (Green et al., 1991), especially in subtropical environments (Olson et al., 1991), beef from *Bos indicus* breeds is less tender than beef from *Bos taurus* cattle (Koch et al., 1982b; Crouse et al., 1989; Van Vleck et al., 1992). Because tenderness is a primary

palatability characteristic considered by consumers (Morgan, et al., 1991), problems with tenderness associated with an increase in *Bos indicus* inheritance must be solved (Crouse et al., 1989).

This study examined the potential of selecting intact or late-castrate males based on their tenderness values for improvement of tenderness of subsequent market progeny. Obtaining semen from males prior to slaughter would allow measurement of tenderness while providing opportunity to select males to sire market progeny with the most tender meat. Exploration of a way to predict breeding values for market-animal tenderness of males capable of producing previously frozen semen, based on their later tenderness measurements, was the goal of this study. In this report, the association between estimates of tenderness in intact males and estimates of tenderness in closely related (e.g., half-sib) steers and heifers is evaluated. A selection experiment involving direct selection for estimates of tenderness in intact males and measurement of tenderness in steer and heifer descendants would provide for a more accurate assessment of this selection scheme. A less costly and

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more immediate assessment, however, is provided by the evaluation of half-sibs and other relatives represented in the present study.

Materials and Methods

Description of the Data

Data were from the Germ Plasm Evaluation (**GPE**) project at the U.S. Meat Animal Research Center (MARC) in Clay Center, Nebraska. Data for the tenderness study came from Cycle I-Phase 2 (1971, 1972) (Koch et al., 1976), Cycle II-Phase 2 (1973, 1974) (Koch et al., 1979), Cycle III-Phase 2 (1975, 1976) (Koch et al., 1982b), Cycle III-Phase 4 (1983–1986) (Crouse et al., 1989), and Cycle III-Phase 5 (1989–1991) of the GPE program. Table 1 shows sire breeds and total number of animals with tenderness measurements in both market animal and potential sire groups.

Group I (Market Animals): Steers and Heifers

Calves were born in March through May and were weaned in October. After weaning, calves were fed a mixed diet for ad libitum intake ranging in energy density from 2.74 Mcal metabolizable energy (ME)/kg dry matter to 2.93 Mcal ME/kg late in the finishing period (Crouse et al., 1989). Steers and heifers were slaughtered between 13 and 15 mo of age.

Group II (Potential Sires): Late-Castrate and Intact Males

Animals born in 1989 and 1990 were part of a study of sex effects on carcass characteristics. Bull calves were weaned according to Group I protocol and fed a diet consisting of 2.83 Mcal ME/kg dry matter until slaughtered. At about 8 mo of age, semen collections were taken monthly until each bull first produced an ejaculate containing $\geq 500 \times 10^6$ sperm with $\geq 50\%$ progressive motility, which was defined as pubertal quality semen (Lunstra, et al., 1993). Such semen is considered to be of freezable quality. Electroejaculation was performed twice at each monthly collection date for each bull. Data for the ejaculate exhibiting the best semen quality were recorded. Semen was collected and maintained at 37°C for evaluation. Progressive motility was determined immediately from duplicate estimates at 37°C, using a microscope (400× magnification). Sperm concentration was determined from spectrophotometer (550 nm) counts of duplicate semen aliquots diluted 1:200 with 1% formalin in .9% saline. Mean age at puberty was 334 d for *Bos taurus* and 404 d for *Bos indicus* bulls (Lunstra et al., 1993).

The experiment was designed so that all sires of Group II bulls had been used in earlier phases of the program, most of which produced a steer or heifer with

Table 1. Number of sires and animals within each sire-breed combination

Sire breed combination	No. of sires	No. of animals
Hereford (H)	13	379
Angus (A)	21	466
Brahman (B)	29	128
Pinzgauer (P)	14	156
Sahiwal (S)	6	155
H × A	14	66
A × H	8	48
B × H	7	21
B × A	5	50
P × H	5	36
P × A	7	55
S × H	6	15
S × A	6	47
AHBS	5	45
Total	147	1,669

carcass data. Inbreeding was avoided in all matings. Thus, bulls that were sires or grandsires of Group I steers and heifers were also sires or grandsires of Group II bulls. No animals were edited out because of lack of relationships between animals in Group I and Group II.

Within each breed combination, when 55% of bull calves had produced semen of pubertal quality, the pubertal bulls were assigned to one of three treatments: 1) to be slaughtered (intact, slaughtered = **IS**); 2) to be castrated and fed an additional 90 d (castrated, fed = **CF**); or 3) to remain intact and be fed an additional 90 d (intact, fed = **IF**). When 90% of the bull calves within each breed combination had produced semen of pubertal quality, all remaining bulls (45%) were assigned randomly to one of the three treatments. Some animals ($\leq 10\%$) never produced semen of pubertal quality.

Measurements: Collection of Tenderness Data

All animals were treated the same within year in both groups. Early in the GPE Program (1971–1976) cooler data were obtained after a 48-h chill. In subsequent years, cooler data were obtained after a 24-h chill. There is no confounding with treatments or sire breed.

Marbling Score

After a 24- to 48-h chill, USDA quality and yield grades were determined. Marbling was evaluated at the 12th rib interface and scored on a 100-point scale within each of seven categories (numeric scale): traces (300), slight (400), small (500), modest (600), moderate (700), slightly abundant (800), and moderately abundant (900). For example, a marbling score (**MS**) of modest 30 is converted to a numeric score of $600 + 30 = 630$.

Table 2. Number of sires and records for shear force, taste panel tenderness, marbling score, and myofibrillar fragmentation index

Tenderness trait/group	No. of sires	No. of records
Shear force (SF)	147	1,668
Late-castrate and intact males	84	237
Steers and heifers	146	1,431
Taste panel tenderness (TPT)	147	1,464
Late-castrate and intact males	84	237
Steers and heifers	146	1,227
Marbling score (MS)	147	1,664
Late-castrate and intact males	84	237
Steers and heifers	146	1,427
Myofibrillar fragmentation index (MFI)	97	436
Late-castrate and intact males	84	237
Heifers	81	199

Shear Force. From 1971 through 1976, the right side of each carcass was transported to Kansas State University for shear force (**SF**) determination and taste panel evaluation (steer carcasses only at that time); in other years, evaluations were performed at MARC. The records were expressed as a ratio to intragroup standard deviations. Thus, the standardization adjusts for any difference in variance associated with procedures used from 1971 to 1976 at Kansas State University and procedures used at MARC in both cooking and shearing methodology (Wheeler et al., 1990). Steaks were removed from the longissimus muscle in the 7th to 11th rib section, aged 7 d, and frozen for Warner-Bratzler shear determination and sensory panel evaluation. Sample preparation followed American Meat Science Association (AMSA, 1978) guidelines. Steaks were thawed 12 to 24 h at 2 to 4°C. From 1971 through 1976 steaks were cooked to an internal temperature of 65°C, cooled for 30 min at room temperature, and cut into eight 1.27-cm-diameter cores for shearing. In following years, steaks were cooked to an internal temperature of 70°C, stored at 5°C for 24 h, and cut into six 1.27-cm cores for shearing. Cores were sheared with an Instron 1132/Microcon II Universal Testing Instrument (Instron Corp., Caton, MA) with a Warner-Bratzler type blade.

Taste Panel Tenderness. Descriptive-attribute sensory panels trained and tested according to methods described by Cross et al. (1978) and AMSA (1978) sampled and scored 1.27-cm cubes, cooked and cored as for shear tests. The taste panel tenderness (**TPT**) scores were based on either a 1 to 9 scale (1 = extremely tough, 9 = extremely tender) or a scale from 1 to 8 for tenderness (1 = extremely tough, 8 = extremely tender). Records were average scores given to each steak by eight panelists.

Myofibril Fragmentation Index. Myofibril fragmentation index (**MFI**) was determined in 1989 and 1990 by a modification of the procedure of Olson et al. (1976), as explained by Culler et al. (1978). Core samples of 1.27 cm were cut from frozen steaks

withheld for analysis. The MFI is a biochemical measure of tenderness predicted by absorbance. Low MFI values are thought to indicate a less tender sample of beef and high MFI values to indicate a more tender sample. Table 2 shows number of animals with measurements for shear force, taste panel tenderness, marbling score, and MFI, and number of sires of animals with records.

Standardization

To minimize rounding error, within each group, each measurement was divided by the overall phenotypic standard deviation (Table 3). Differences in variation also were found among years due to different evaluation procedures and locations. Therefore, across groups and within trait, each record was standardized by dividing by the phenotypic standard deviation associated with the year the record was taken (Table 3).

Estimates of Genetic Parameters and Breed Effects for Tenderness Traits of Market Animals

Multiple-trait sire models were used for separate analyses of Group I and Group II data. Estimates of genetic and environmental (co)variances and breed effects were obtained with a derivative-free restricted maximum likelihood algorithm (Smith and Graser, 1986; Meyer, 1991).

Fixed effects for tenderness traits of Group I included 13 yr (1971–1976, 1983–1986, 1989–1991), sex (steer, heifer), and 18 fixed covariates. Covariates included weaning age, number of days on feed, five breed fractions (A, H, P, B, S), five sex × breed interactions, expected heterozygosity level for direct effects, and five heterozygosity level × breed interactions. The only random effect in the model other than residual was the transmitting ability of the sire. Sires were assumed to be unrelated for these analyses.

Table 3. Phenotypic standard deviations used to standardize shear force (SF), taste panel tenderness (TPT), marbling score (MS), and myofibrillar fragmentation index (MFI)^a

Standardization type	SF	TPT	MS	MFI
Scale				
Group I	2.100	1.370	95.2	17.5
Group II	1.843	.972	50.8	19.8
Year				
1971	1.029	.479	1.186	—
1972	.700	.466	.913	—
1973	.800	.693	1.236	—
1974	1.155	.658	1.149	—
1975	1.025	.899	1.213	—
1976	.876	.816	.925	—
1983	1.020	.409	.819	—
1984	.887	.409	.816	—
1985	.862	.511	.641	—
1986	.808	.512	1.219	—
1989	.859	1.161	1.684	1.015
1990	.961	1.109	1.534	.916
1991	.750	.581	.692	—

^aFor example, standardized shear force = SF ÷ Group standard deviation ÷ Year standard deviation; e.g., a Group I shear force value of 3.6 in 1989 would have a standardized value of $3.6 \div 2.1 \div .859 = 1.996$.

The model for tenderness traits of Group II included effects for 2 yr (1989 and 1990) and three sex classes (CF, IF, and IS). All interactions as listed for Group I in the preliminary models were found to be nonsignificant and were dropped from the final model for both Group I and Group II.

(Co)variance components for each group were estimated for a sire model with the multiple-trait derivative-free REML program (**MTDFREML**) of Boldman et al. (1993). The (co)variance components at initial convergence were used as starting values for a restart with convergence criterion 1×10^{-9} . This process was repeated until minus twice the logarithm of the likelihood for two successive restarts differed by less than 1×10^{-4} . The solutions for (co)variance components from the last restart were converted to the original scale by pre- and post-multiplying the standardized estimates first by the diagonal matrix of the raw phenotypic standard deviations used to standardize the measurements of each trait for each group and second by the diagonal matrix of raw phenotypic standard deviations associated with the year 1989 (Table 3).

An approximate method of finding the associated standard errors was based on the method of Swiger et al. (1964), which is expected to underestimate the actual standard errors.

Genetic correlations between same named traits of animals in Group I and Group II were calculated as the sire component of covariance between the groups divided by the product of the estimated standard deviations of sire effects of the two groups.

Regression coefficients for breed additive effects were multiplied first by the raw phenotypic standard

deviations used for standardizing each corresponding trait and second by the phenotypic standard deviation used to standardize to the year 1989 to obtain estimates on the original scale and are denoted here as breed effects. The Hereford covariate was constrained to zero.

Mixed-Model Procedure to Predict Breeding Values

Development of an evaluation method for selection of bulls based on their own tenderness measurements to improve market-animal tenderness involved two steps. First, (co)variance components were estimated among the traits of Group II animals and the desired trait in animals of Group I. Data were analyzed using two five-trait sire models. The first analysis included all Group II tenderness measurements (SF, TPT, MS, MFI), as well as market animal (Group I) TPT, represented in the equations as TPT*. The second analysis included the same Group II measurements and Group I SF (represented as SF*). The analysis was concluded when minus twice the logarithm of the likelihood from the final two starts differed by less than 1×10^{-4} .

The second step was to predict breeding values of the bulls for tenderness of market animals through the use of an animal model. In practice, steer and heifer records would not be available, so a method is needed to predict breeding values for a trait, when all records on that trait are missing, e.g., TPT* or SF*. One method described by Henderson (1977) has been demonstrated by Barkhouse and Van Vleck (1994). In the mixed-model equations, the incidence matrix for

Table 4. Regression coefficients (1989 basis) for direct additive breed effects for shear force (SF), taste panel tenderness (TPT), marbling score (MS), and myofibrillar fragmentation index (MFI)

Breed	SF, kg group		TPT, units group		MS, units group		MFI, index units group	
	I ^a	II ^a	I	II	I	II	I	II
Hereford	0 ^{bc}	0 ^b	0 ^b	0 ^b	0 ^b	0 ^d	0 ^{bc}	0 ^b
Angus	-.15 ^b	-1.06 ^b	.50 ^c	.61 ^c	117 ^c	35 ^c	4.1 ^b	-2.2 ^b
Pinzgauer	.43 ^c	-.01 ^b	-.14 ^b	.08 ^b	-119 ^d	-34 ^d	-1.5 ^{bc}	-6.0 ^b
Brahman	2.47 ^d	2.47 ^c	-1.95 ^d	-1.29 ^d	-210 ^e	-74 ^d	-10.1 ^c	-11.3 ^b
Sahiwal	4.15 ^e	4.24 ^c	-3.25 ^e	-2.32 ^e	-175 ^{de}	-70 ^d	-49.5 ^d	-48.0 ^c

^aI = Group I: steers and heifers; II = Group II: late castrates and intact males.

^{b,c,d,e}Coefficients within a column possessing the same superscript do not differ ($P < .05$).

transmitting abilities, \mathbf{Z} , is augmented with rows of zeroes representing all animals for the missing fifth trait, either TPT* or SF* scores. The equations for the corresponding animal model are:

$$\begin{bmatrix} \mathbf{y}_{\text{SF}} \\ \mathbf{y}_{\text{TPT}} \\ \mathbf{y}_{\text{MS}} \\ \mathbf{y}_{\text{MFI}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{\text{SF}} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_{\text{TPT}} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{X}_{\text{MS}} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{X}_{\text{MFI}} \end{bmatrix} \begin{bmatrix} \beta_{\text{SF}} \\ \beta_{\text{TPT}} \\ \beta_{\text{MS}} \\ \beta_{\text{MFI}} \end{bmatrix} +$$

$$\begin{bmatrix} \mathbf{Z}_{\text{SF}} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_{\text{TPT}} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_{\text{MS}} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{Z}_{\text{MFI}} & \mathbf{0} \end{bmatrix} \begin{bmatrix} \mathbf{u}_{\text{SF}} \\ \mathbf{u}_{\text{TPT}} \\ \mathbf{u}_{\text{MS}} \\ \mathbf{u}_{\text{MFI}} \\ \mathbf{u}_{\text{TPT}^*} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{\text{SF}} \\ \mathbf{e}_{\text{TPT}} \\ \mathbf{e}_{\text{MS}} \\ \mathbf{e}_{\text{MFI}} \end{bmatrix}$$

where the \mathbf{u} vectors are animal genetic values. The \mathbf{X} and \mathbf{Z} matrices for SF, TPT, MS, and MFI may be different based on whether records are available for each trait.

The data included only records on Group II males related through their sires. The multiple-trait mixed model equations are:

$$\begin{bmatrix} \mathbf{X}'\mathbf{E}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{E}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{E}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{E}^{-1}\mathbf{Z} + \mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \beta \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{E}^{-1}\mathbf{Y} \\ \mathbf{Z}'\mathbf{E}^{-1}\mathbf{Y} \end{bmatrix}$$

with $\mathbf{E}^{-1} = \mathbf{E}_0^{-1} \otimes \mathbf{I}$ and $\mathbf{G}^{-1} = \mathbf{G}_0^{-1} \otimes \mathbf{A}^{-1}$, where \otimes is the direct product operator. Estimates of the environmental and genetic covariance matrices among traits on the same animal, \mathbf{E}_0 and \mathbf{G}_0 , were obtained from (co)variance components estimated with the previously described sire model analyses which included measurements on Group I and Group II animals. All bulls in Group II and their sires were included in \mathbf{A} , the numerator relationship matrix. The genetic covariance matrix $\mathbf{G} = \mathbf{G}_0 \otimes \mathbf{A}$ ties the measured traits on Group II males (Henderson, 1977) to their genetic values as market animals.

Estimated breeding values of Group II bulls and their sires for TPT* or SF* as market animals were

calculated through the solve option of the MTDFREML program to obtain five estimated breeding values for each potential sire: SF as a bull, TPT as a bull, MS as a bull, MFI as a bull, and TPT* or SF* as if the male had been a market animal (steer or heifer). Solutions for TPT* or SF* would be the basis for selection of males with previously frozen semen to improve market animal tenderness.

Results and Discussion

Breed effects on the original scale were obtained from multiplying the solutions for the regression coefficients for breed fractions in the multiple-trait mixed-model equations by the raw phenotypic standard deviations used to standardize the records. Table 4 shows breed effects for SF, TPT, MS, and MFI relative to Hereford.

Rankings for breed effects were similar for Group I and Group II. For all traits, the *Bos taurus* breeds ranked as more desirable than the *Bos indicus* breeds, but the differences were not all significant for MS and MFI. Compared to Brahman inheritance Sahiwal had significantly less implied tenderness for SF, TPT, and MFI, but Brahman and Sahiwal were not different for MS. These results agree with previous reports (Cover et al., 1957; Burns et al., 1958; Damon et al., 1960; Ramsey et al., 1963; Gregory et al., 1978; Crockett et al., 1979; Koch et al., 1982b; Peacock et al., 1982; Crouse et al., 1989; Wheeler et al., 1990; Shackelford et al., 1991; and Whipple et al., 1990).

Covariances Among Group I and Group II Tenderness Traits

Estimates of heritability and variance components for SF, TPT, MS and MFI for Group I and Group II are shown in Table 5. Group I traits were more variable, phenotypically, than Group II traits, especially for MS. These results do not agree with Reagan et al. (1971), who found greater variation in shear force and taste panel tenderness scores for bulls than for steers.

Table 5. Estimates from separate analyses for Group I and Group II animals of additive genetic, residual, and phenotypic variance components and heritability for shear force (SF), taste panel tenderness (TPT), marbling score (MS), and myofibrillar fragmentation index (MFI)^{a,b}

Variance	SF		TPT		MS		MFI	
	I ^c	II ^c	I	II	I	II	I	II
Genetic ^d	.061	.545	.107	.017	7,416	329	142	39
Environmental	2.450	1.468	1.634	.643	10,944	1,410	104	200
Phenotypic	2.511	2.013	1.741	.660	18,360	1,739	246	239
Heritability	.02 ± .06	.27 ± .29	.06 ± .07	.03 ± .28	.40 ± .08	.19 ± .29	.58 ± .35	.17 ± .29

^aVariances are on a 1989 basis.

^bUnits for SF = kg², TPT = units², MS = units², and MFI = index units².

^cI = Group I: steers and heifers; II = Group II: late castrates and intact males.

^dGenetic = 4 × sire component.

Previous heritability estimates for SF have ranged from 0.00 to 1.29 and averaged .27 (Alsmeyer et al., 1958; Busch and Dinkel, 1967; Dinkel and Busch, 1973; Wilson et al., 1976; Koch et al., 1982a; Shackelford et al., 1991; Van Vleck et al., 1992; Gregory et al., 1994). The estimate for SF in Group I of .02 was less than the average heritability estimate in the literature (.27), which may be due to sampling variance. The heritability estimate of SF for Group II was the same as the average estimate in the literature. The Group II estimate, however, is based on one-fifth of the number of records available for steers and heifers. The approximate standard errors calculated for these heritability estimates suggest that neither estimate is significantly different from zero. The approximate standard error for the Group I estimate was .06, and the standard error for the Group II estimate was nearly five times larger (.29).

Van Vleck et al. (1992) reported a heritability estimate of .12 for TPT, Wilson et al. (1976) reported an estimate of .23, and Gregory et al. (1994) reported an estimate of .22. Standard errors were similar to those for SF for Group I and for Group II.

The heritability estimate of MS for Group I was significantly different from zero (.40 ± .08), which agrees with estimates by Wilson et al. (1976) and Benyshek (1981) for steer and heifer marbling scores. Other studies have shown marbling to be moderately to highly heritable, with estimates ranging from .31 to

.82 and averaging .45 (e.g., Koch et al., 1982a). Lamb et al. (1990) reported an estimate of .39 in Hereford bulls. The estimate for Group II of .19 ± .29, although not significantly different from zero, may indicate that MS may not be as heritable for late castrates and intact males as for steers and heifers. A reviewer suggests that marbling in late castrate and intact males may not be the same physiological character as in steers and heifers.

Heritability estimates for MFI in Groups I and II were .58 and .17, respectively. Heritability estimates for MFI have not been reported previously. The standard errors for MFI in Group I were larger than for SF, TPT, or MS because only heifer data were available for MFI. The Group I and Group II estimates of heritability were not significantly different from zero.

Estimates of genetic and phenotypic correlations among the tenderness traits for Group I and Group II are within the range of previous estimates (Table 6). Estimates of genetic correlations between SF and TPT were highly negative in both Group I and Group II, -.60 and -.67, respectively. Other studies reported estimates ranging from -.54 to -.93 (Wilson et al., 1976; and Hakim et al., 1990). Shear force and MFI were highly negatively correlated ($r_g = -.63$), whereas TPT and MFI were positively correlated in Group I ($r_g = .63$). Phenotypic correlations between MFI and SF ranging between -.65 and -.97 have been reported, as

Table 6. Estimates from separate analyses for Group I and Group II animals of genetic (phenotypic) correlations among shear force (SF), taste panel tenderness (TPT), marbling score (MS), and myofibrillar fragmentation index (MFI) for Groups I and II^a

Item	SF	TPT	MS	MFI
SF	—	-.60 (-.98)	-.60 (-.50)	-.63 (-.87)
TPT	-.67 (-.86)	—	.17 (.64)	.63 (.77)
MS	-.18 (-.96)	.22 (.73)	—	-.09 (.01)
MFI	-.52 (.21)	.50 (.52)	.10 (-.17)	—

^aGroup I correlations are above the diagonal; Group II correlations are below the diagonal.

Table 7. Estimates of heritability with standard errors and of variance components for joint analysis of Group II traits (shear force [SF], taste panel tenderness [TPT], marbling score [MS], and myofibrillar fragmentation index [MFI]) and Group I taste panel tenderness (TPT*)

Component	SF	TPT	MS	MFI	TPT*
Genetic	.619	.01	324	46.0	.174
Environmental	1.384	.64	1,411	194.1	1.527
Phenotypic	2.003	.66	1,735	240.1	1.701
Heritability	.31 ± .29	.02 ± .28	.19 ± .29	.19 ± .29	.10 ± .06

well as phenotypic correlations between MFI and TPT ranging from .65 to .95 (MacBride et al., 1977; Olson and Parrish, 1977; and Culler et al., 1978). Marbling score was positively correlated with SF, TPT, and MFI.

Combined Analysis for Market Animal Taste Panel Tenderness

The estimates of (co)variance components in Table 7 are after 14 restarts to ensure the global maximum of the likelihood was attained. Estimates of heritability for Group II traits in the combined analysis were not expected to be, and were generally not, different from those from analysis of Group II traits alone. The genetic correlations differed slightly (Table 8). The largest difference was for $r_{TPT,MFI}$ ($r_g = -.27$) compared to the Group II analysis ($r_g = .52$). Estimates of genetic variation for TPT and MFI did not differ greatly between the two analyses, although the sign of the covariance between these traits changed. These differences may be due to the amount of data. When the Group I trait was analyzed with the four Group II traits, the large number of animals in Group I seemed to influence the estimates of (co)variance components among the Group II traits. In the combined analyses the covariances between the traits on bulls and the trait on market animals are based mostly on different half-sibs, with most measurements on the trait of the market animals (except for MFI) in contrast to analyses of Group I and Group II, for which most animals have measurements on all traits (except MFI for Group I animals).

The estimate of heritability for Group I TPT* was .10, close to the estimate of .06 obtained from the

analysis in Group I. Neither estimate, however, was significantly different from zero. As expected, TPT* of steers and heifers was favorably correlated genetically to SF ($r_g = -.37$) and TPT ($r_g = .79$) of intact males, indicating that SF or TPT measured on bulls should be a good indicator of market-animal (steer and heifer) TPT. Genetic correlations of TPT* with MS and MFI, however, were negative.

*Breeding Values of Bulls for Market-Animal TPT**

Breeding values of bulls for TPT of a market animal can be predicted through the use of mixed-model methodology as described earlier. The E_0 and G_0 matrices used for prediction of breeding values with an animal model were with traits in order (SF, TPT, MS, MFI, and TPT* for G_0):

$$E_0 = \begin{bmatrix} 1.384 & -.686 & 1.406 & -11.764 \\ -.686 & .643 & 6.194 & 6.554 \\ 1.406 & 6.194 & 1411.100 & 68.870 \\ -11.764 & 6.554 & 68.870 & 194.130 \end{bmatrix}$$

$$G_0 = \begin{bmatrix} .619 & -.082 & -12.200 & .475 & -.122 \\ -.082 & .015 & 1.077 & -.222 & .040 \\ -12.200 & 1.077 & 324.060 & -5.020 & -1.072 \\ .475 & -.222 & -5.020 & 46.000 & -.763 \\ -.122 & .040 & -1.072 & -.763 & .174 \end{bmatrix}$$

There were 361 animals in the analysis (237 Group II bulls, and 124 sires of the bulls).

The predicted breeding values within breed ranged from $-.11$ to $.08$, with most animals predicted to be

Table 8. Estimates of genetic and phenotypic correlations from joint analysis of Group II tenderness traits (shear force [SF], taste panel tenderness [TPT], marbling score [MS], myofibrillar fragmentation index [MFI]) and Group I taste panel tenderness (TPT*)^a

Trait	SF	TPT	MS	MFI	TPT*
SF	—	-.86	-.86	.09	-.37
TPT	-.67	—	.49	-.27	.79
MS	-.18	.22	—	-.04	-.14
MFI	-.52	.50	.10	—	-.27

^aGenetic correlations are above the diagonal; phenotypic correlations are below the diagonal.

Table 9. Estimates of heritability with standard errors and of variance components from joint analysis of Group II traits (shear force [SF], taste panel tenderness [TPT], marbling score [MS], and myofibrillar fragmentation index [MFI] and Group I taste panel tenderness (SF*))

Component	SF	TPT	MS	MFI	SF*
Genetic	.630	.01	265	49.5	.108
Environmental	1.391	.64	1,469	189.3	2.399
Phenotypic	2.021	.65	1,734	238.8	2.507
Heritability	.31 ± .29	.02 ± .28	.15 ± .28	.21 ± .29	.04 ± .06

close to zero. Prediction error variances (**PEV**) for the breeding values were approximately .15. Accuracy, a measure of relationship between true breeding value and its prediction, was approximately .36 as calculated from BIF guidelines: $\sqrt{1 - (\text{PEV}/\sigma_{g\text{TPT}^*}^2)}$. The small accuracies associated with this method are primarily a result of the low estimate of heritability and information only on the bulls.

The interbreed predicted breeding values obtained by adding the corresponding breed effects to the within-breed breeding values ranged from -1.10 to .20. The Angus-Hereford-cross bulls had the highest breeding values, following by the Pinzgauer crosses. Brahman and Sahiwal crosses with Angus or Hereford had lowest breeding values for market-animal taste panel tenderness.

Combined Analysis for Market Animal Shear Force

Estimated variance components after 12 restarts are given in Table 9. Estimates of heritability from this analysis were similar to those found in both the Group II and the combined TPT* analyses. The same pattern of genetic correlations as with the combined TPT* analysis (Table 10) was expected because the two analyses differed only in the fifth trait (TPT* or SF*). Shear force in market animals, SF*, was negatively correlated with Group II TPT ($r_g = -.46$) and MS ($r_g = -.04$), but was highly positively correlated with MFI ($r_g = .99$), indicating that improvement in SF would be accompanied by a decrease in MFI.

The estimate of heritability for SF*, .04, was similar to the estimate of .02 obtained from the Group I analysis and was not significantly different from zero. The genetic correlation of SF* with Group II SF was positive but small ($r_g = .17$).

Breeding Values of Bulls for Market Animal Shear Force

The \mathbf{E}_0 and \mathbf{G}_0 matrices were:

$$\mathbf{E}_0 = \begin{bmatrix} 1.391 & -.692 & .803 & -11.720 \\ -.692 & .642 & 6.182 & 6.580 \\ .803 & 6.182 & 1469.200 & 61.940 \\ -11.720 & 6.580 & 61.940 & 189.310 \end{bmatrix}$$

$$\mathbf{G}_0 = \begin{bmatrix} .630 & -.079 & -12.010 & .387 & .045 \\ -.079 & .013 & 1.213 & -.296 & -.017 \\ -12.010 & 1.213 & 264.630 & -6.052 & -.235 \\ .387 & -.296 & -6.052 & 49.500 & 2.293 \\ -.045 & -.017 & -.235 & 2.293 & .108 \end{bmatrix}$$

The within-breed predicted breeding values for SF* ranged from -.34 to .32 units. The average PEV was approximately .08, resulting in an accuracy of prediction of .47. The predictions of interbreed breeding values for Group II animals had a much larger range (-.24 to 2.64) due to large breed differences than the within-breed predictions. As with the predicted breeding values for TPT*, the *Bos taurus* crosses had the most desirable breeding values. The *Bos indicus* crosses had the highest (least desirable) breeding values for SF*.

Table 10. Estimates of genetic and phenotypic correlations from joint analysis of Group II tenderness traits (shear force [SF], taste panel tenderness [TPT], marbling score [MS], myofibrillar fragmentation index [MFI] and Group I shear force (SF*))^a

Trait	SF	TPT	MS	MFI	SF*
SF	—	-.88	-.93	.07	.17
TPT	-.67	—	.66	-.37	-.46
MS	-.19	.22	—	-.05	-.04
MFI	-.52	.50	.11	—	.99

^aGenetic correlations are above the diagonal; phenotypic correlations are below the diagonal.

Implications

Modified mixed-model equations used in the solve option of MTDFREML can be used to compute breeding values quickly and easily for traits without measurements, such as market animal tenderness, using measurements on other traits of bulls. The genetic correlation between taste panel tenderness (TPT) of males and TPT of market animals was high, .94, indicating that selection of intact or late castrate males based on high TPT scores would result in improved TPT in their steer and heifer offspring. Estimates of heritability of TPT, however, were low, ranging from .02 to .06, and not differing significantly from zero. With heritability nearly zero, there is essentially no genetic variation. Because response to selection requires genetic variation, within-breed selection for TPT would result in little change in TPT scores. If the mean of heritability estimates reported in the literature of .27 for shear value was assumed for market steer and heifer progeny instead of .02 found in the present study, then selection for estimates of shear force in young bulls (heritability of .27) would be relatively effective in improving shear force of market animals.

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